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WOOD ANATOMY OF *PLAKOTHIRA* (LOASACEAE)

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ABSTRACT

Wood anatomy of the single species of *Plakothira*, a recently discovered genus from the Marquesas Islands, is described qualitatively and quantitatively. Features new for the family include presence of vasicentric scanty axial parenchyma and presence of perforated ray cells. *Plakothira* has several wood features specialized for Loasaceae: vasicentric axial parenchyma, extremely reduced borders on fiber-tracheids, and storying in fiber-tracheids. Wood of *Plakothira* is clearly loasaceous. Storying in fiber-tracheids is reported here for the loasaceous genera *Fuertesia* and *Mentzelia*. Wood anatomy of *Plakothira* represents paedomorphosis in great length of vessel elements, erectness of ray cells, lack of change in large primary rays, and in presence of occasional scalariform perforation plates. *Plakothira* has wood features maximally mesomorphic for the family, correlating with its cloud-forest habitat and semisucculent wood and cortex structure.

Key words: Loasaceae, *Plakothira*, paedomorphosis, storied wood structure, wood anatomy.

INTRODUCTION

A survey of wood anatomy of Loasaceae (Carlquist 1984a) included all of the woody genera known at that time. A year later, however, a new woody genus, *Plakothira*, was added to the family by Florence (1985). This genus is of considerable interest because it represents an extension of the family into the Pacific; the family is otherwise native to North and South America with a single genus, *Kissenia* (sometimes cited as *Fissenia*), from Africa and Arabia (Florence 1985). *Plakothira* is known only from Nukuhiva, Marquesas Is., where it forms a sparsely-branched rosette shrub (to 3 m) in the *Crossostylis-Cyathea* cloud forest.

Plakothira has been placed by Florence (1985) in the tribe Klaprothieae, although resemblances to tribes Loaseae and Mentzelieae are noted. Because there is a range in wood anatomy within Loasaceae in which distribution of certain features corresponds to the taxonomic system (Carlquist 1984a), some wood data pertinent to systematic placement of *Plakothira* are available.

The tallness and the sparsely branched habit of *Plakothira*, as well as the predominantly herbaceous nature of the family and the insular nature of the genus suggest that *Plakothira* may be secondarily woody. If so, one would expect indicators of paedomorphosis in wood anatomy: persistence with little modification of metaxylem features into secondary xylem (Carlquist 1962), and attention is paid to this phenomenon in the present study.

The habitat of *Plakothira* seems more mesic than that of other Loasaceae, because in the family ecological preferences otherwise range from seasonally dry to desertlike. Because wood anatomy is often a sensitive indicator of ecology, wood data known to be indicators of ecology are examined for *Plakothira*.

MATERIALS AND METHODS

Samples representing basal portions of a plant of *Plakothira frutescens* Florence were fixed in formalin-acetic-alcohol and kindly supplied to me by M. J. Florence of ORSTOM, Papeete, Tahiti. The wood sample represents a basal stem about 4.5 cm in diameter as well as some upper stems. The data reported here apply to the basal stem only because sections and macerations of the upper stem revealed no differences from features observed in the basal stem. Sections were prepared on a sliding microtome. Large cell size resulted in considerable fracturing of cell walls when sectioning was attempted at 20–26 μm , but sections at 30 μm proved acceptable. Because cells of *Plakothira* are relatively large compared to those of most woods, the thicker sections were not disadvantageous for study of histology. Sections were stained in a safranin-fast green combination. Macerations were prepared by means of Jeffrey's Fluid and stained with safranin. Vessel diameter was measured as diameter of lumen at the widest point in a vessel as seen in transection. Means given for features in the descriptions below were obtained from 25 measurements except for vessel wall thickness, fiber-tracheid diameter, and fiber-tracheid wall thickness; in these three features, a few typical cells were selected for measurement. The herbarium specimen voucher for the collection studied is cited by Florence (1985).

ANATOMICAL DESCRIPTION

PLAKOTHIRA FRUTESCENS (Florence 6774) (Fig. 1–10).—Growth rings absent (Fig. 1). Vessels mostly solitary or in radial multiples or clusters of very limited extent (Fig. 1). Mean number of vessels per group, 1.16. Mean vessel diameter, 92 μm . Mean number of vessels per mm^2 , 5.4. Mean vessel element length, 530 μm . Mean vessel wall thickness, 2.1 μm . Perforation plates simple (except for perforated ray cells mentioned below). Lateral wall pitting of vessels consists of oval alternate pits with unusually wide (“gaping”) apertures as shown in Fig. 5–8. Vessel-vessel pits (Fig. 5–7) typically about $6 \times 8 \mu\text{m}$, vessel to fiber-tracheid pits about $8 \times 10 \mu\text{m}$, and vessel-axial parenchyma pits about $9 \times 14 \mu\text{m}$ (Fig. 8). Some intervacular pitting pseudoscalariform by virtue of lateral widening of alternate pits (Fig. 7). All imperforate tracheary elements may be termed fiber-tracheids because pits possess extremely small borders; pit apertures are small and slitlike, about 2 μm in length (Fig. 4). Fiber-tracheids are all nucleated and nonseptate. Mean fiber-tracheid diameter at widest point, 39 μm . Mean fiber-tracheid length, 985 μm . Mean fiber-tracheid wall thickness, 2.4 μm . Axial parenchyma vasicentric scanty, forming sheaths 1–2 cells wide around vessels or vessel groups; vessels in contact with fiber-tracheids very rarely. No diffuse parenchyma present. Axial parenchyma in strands of two (rarely three) cells. Rays both multiseriate and uniseriate (Fig. 2, 3), but uniseriate rays are few and seem the results of recent subdivision of fusiform cambial initials (Fig. 2, center). Multiseriate rays composed of erect cells almost exclusively; square cells few, procumbent cells the product of horizontal divisions of ray cells. Ray cells with lignified walls bearing small simple pits; more elongate ray cells tend to resemble fiber-tracheids in wall thickness and shape. Mean height of multiseriate rays more than 5 mm (a mean figure could not be determined on the basis of sectioned material). Mean multiseriate ray width, 10.2 cells. Mean uniseriate ray height, 296 μm . Perforated ray cells present, either with simple plates (Fig. 9, below) or with scalariform plates

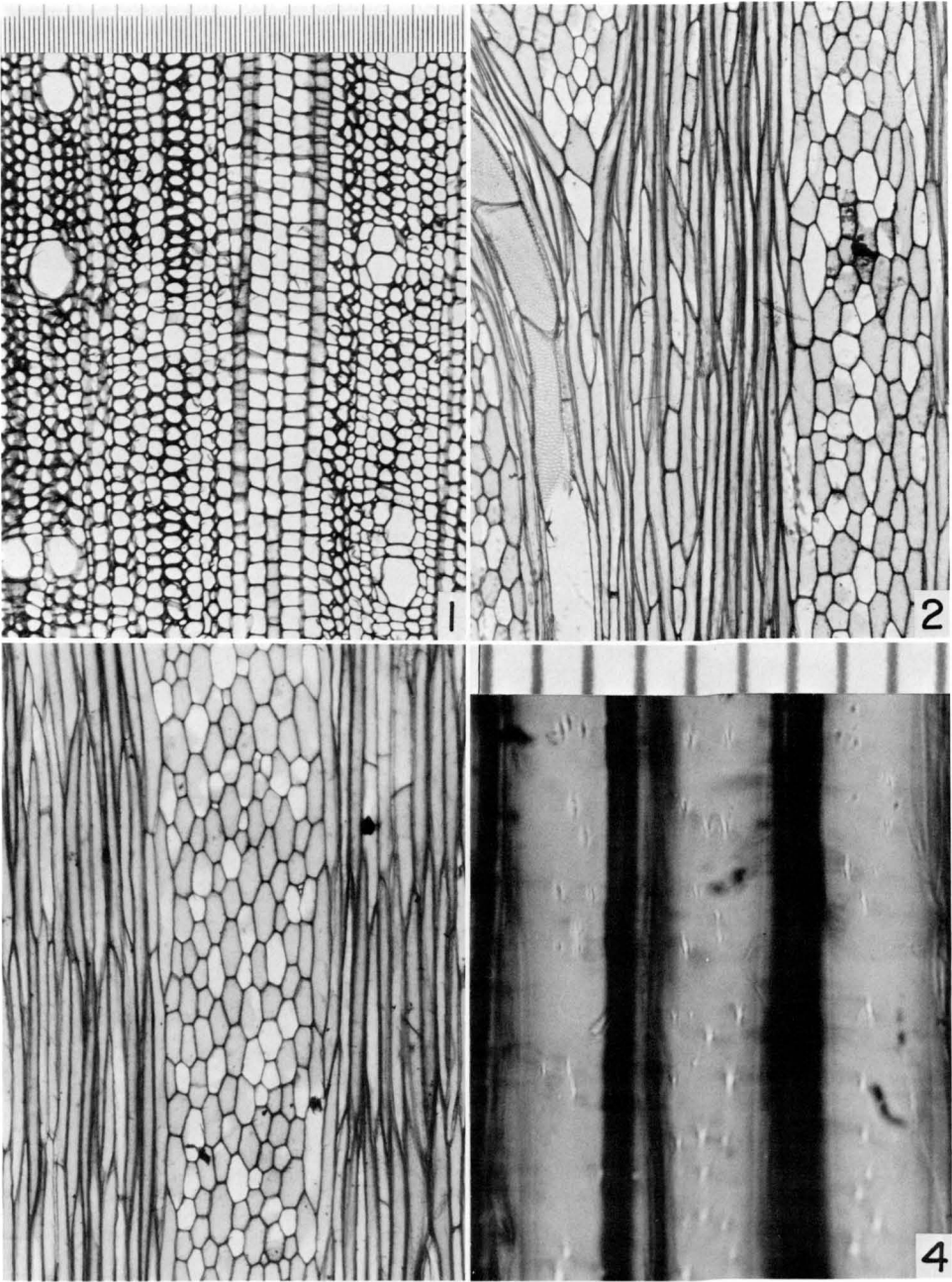


Fig. 1-4. Wood sections of *Plakothira frutescens* (Florence 6774).—1. Transection; vessel density is low.—2. Tangential section; uniseriate rays may be seen in zone of fiber-tracheids, center.—3. Tangential section showing multiseriate ray, center, with stored fiber-tracheids to left and right of it.—4. Fiber-tracheids from radial section, showing slitlike pit apertures (pit borders not visible). (Magnification scale for Fig. 1-3 above Fig. 1 [finest divisions = 10 μ m]; scale for Fig. 4 above Fig. 4 [divisions = 10 μ m].)

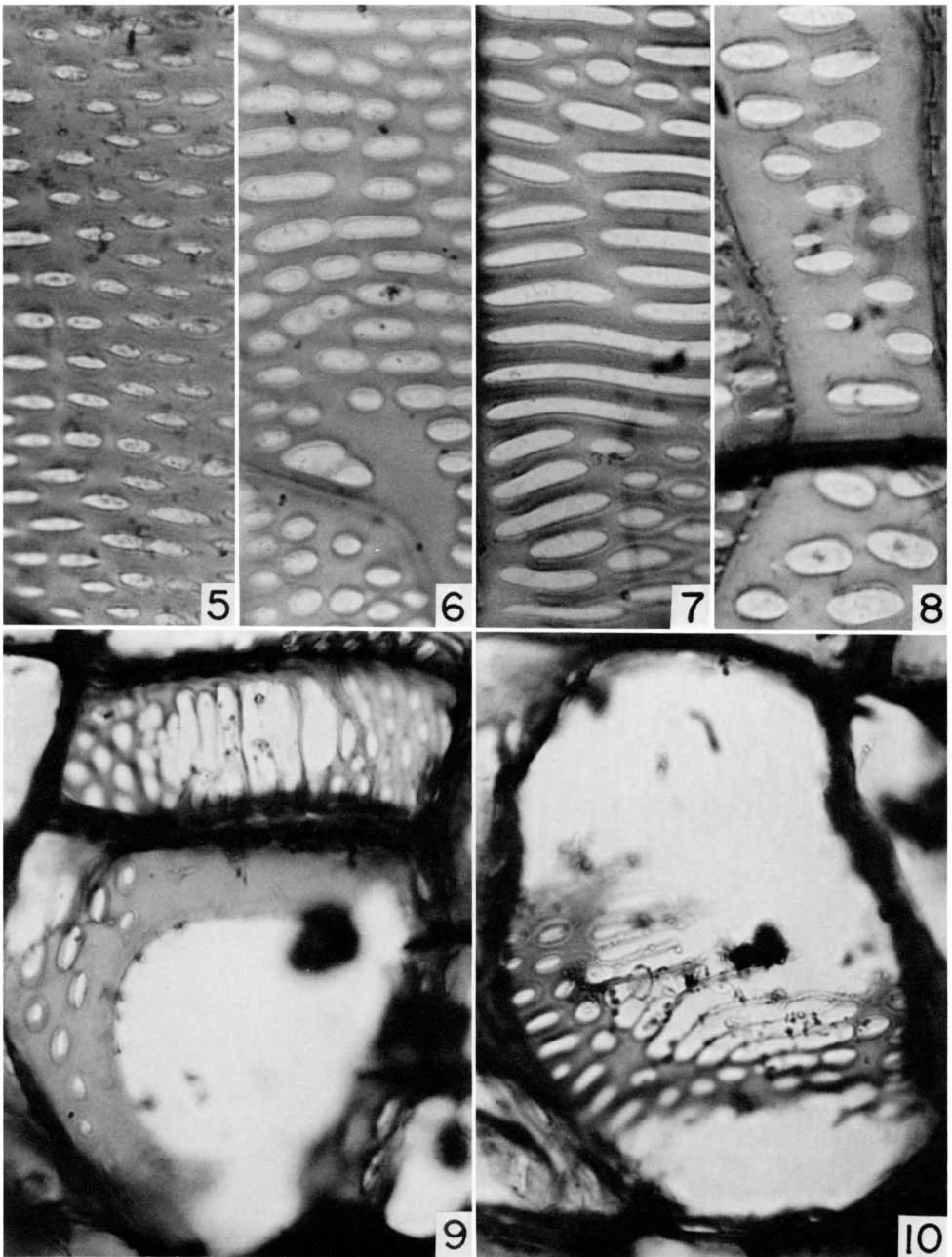


Fig. 5-10. Wood sections of *Plakothira frutescens* (Florence 6774).—5-7. Vessel-vessel pitting from tangential sections.—5. Pits relatively small in size.—6. Pits of intermediate size.—7. Pseudo-scalariform pits.—8. Vessel-axial parenchyma pitting from radial section.—9-10. Perforated ray cells from radial section.—9. Two perforated ray cells: the one below with a simple perforation plate, the one above with modified scalariform plate.—10. Perforated ray cell in which a scalariform perforation plate (part of it cut away) is present. (Fig. 5-10, magnification scale above Fig. 4.)

(Fig. 9, above; Fig. 10) modified somewhat by interconnections among the bars. Fiber-tracheids storied in some places (Fig. 3), storying not evident in other places of the same age (Fig. 2). No crystals present in wood. Very small starch grains occasional in ray cells.

DISCUSSION AND CONCLUSIONS

Systematics

Plakothira frutescens has some features not hitherto reported for Loasaceae. Axial parenchyma is vasicentric scanty in *Plakothira*, whereas only diffuse (abundant to scarce), banded, and pervasive (parenchyma replaces all or large proportion of potential zones of imperforate tracheary elements) types have thus far been reported from Loasaceae (Carlquist 1984a). This would seem a very distinctive feature, because in many families of dicotyledons, axial parenchyma types vary relatively little. The vasicentric pattern of axial parenchyma in *Plakothira* can be interpreted as a specialization over the diffuse condition in the remainder of the family according to the work of Kribs (1937). The other feature newly reported for Loasaceae on the basis of *Plakothira*, presence of perforated ray cells, is of less importance because perforated ray cells occur in a scattering of dicotyledonous woods without any apparent relationship to the taxonomic system.

The other wood features of *Plakothira* mark it clearly as a member of Loasaceae, but specialized within that family. The imperforate tracheary elements have pits with vestigial borders; although the borders are very small, these cells are termed fiber-tracheids here in accordance with the IAWA Committee on Nomenclature (1964). In other genera of Loasaceae, such as *Eucnide* and *Fuertesia*, border diameter can reach 5 μm in imperforate tracheary elements, and those cells lie on the borderline between tracheids and fiber-tracheids (Carlquist 1984a). The genera of Loasaceae with vestigial borders on fiber-tracheid pits are all Southern Hemisphere genera: *Loasa* and *Kissenia* (sometimes cited as *Fissenia*). This is a logical distribution for this character phytogeographically, because *Plakothira* would be expected to be derived from ancestors in South America, where *Loasa* is native. The "gaping" nature of pit apertures on lateral vessel walls in *Plakothira* is a feature common in Loasaceae. The perforation plates of *Plakothira* are simple, consistent with Loasaceae (exceptions discussed below). Axial parenchyma is present as strands of two cells in *Plakothira*, as it is in the remainder of the family. The rays of *Plakothira* are like those of other Loasaceae in being mostly multi-seriate, tall, and wide; uniseriate rays are never common in Loasaceae and some species lack them altogether (Carlquist 1984a). Ray cells in *Plakothira* have thin but lignified walls, a feature typical of other Loasaceae. Ray cells in *Plakothira* are predominantly erect, with square cells uncommon and present usually by subdivision of occasional erect ray cells; such ray histology is common in Loasaceae (notably *Loasa incana* R. & P.). Dimensions of vessel elements and fiber-tracheids in *Plakothira* are large for dicotyledons as a whole, but these cell types are also large in other Loasaceae (Carlquist 1984a). Cell size does not seem to relate to degree of specialization in *Plakothira*.

Plakothira is notable for presence of storied fiber-tracheids. Storied structure was not mentioned in the survey of Loasaceae (Carlquist 1984a), although storied

fiber-tracheids and uniseriate rays are evident in the tangential section of *Fuertesia* illustrated in that paper. Examination of other Loasaceae with relatively old stems (in which storying would be expected to be more prevalent than it is in younger stems) revealed presence of storied fiber-tracheids and axial parenchyma cells in *Mentzelia arborescens* Urban & Gilg. Storied wood structure should be regarded as a specialized feature within Loasaceae, in accordance with the interpretation of Bailey (1923).

Among the woody Loasaceae studied to date, *Plakothira* shows more resemblance to *Loasa* than to the other genera. This is by no means rules out placement in tribe Klaprothieae as advocated by Florence (1985). No Klaprothieae were included in my earlier study or in this one because of the entirely herbaceous nature of Klaprothieae other than *Plakothira*. Loaseae and Mentzelieae are mentioned by Florence as tribes to which *Plakothira* may also be close.

Habit

Plakothira has mean vessel element length somewhat longer (530 μm) than that of the vine *Fuertesia* (477 μm), but mean fiber-tracheid length shorter (985 μm) than that of *Fuertesia* (1165 μm); *Fuertesia* has the longest vessel elements and fiber-tracheids hitherto reported for the family (Carlquist 1984a). *Plakothira* probably has fusiform cambial initials longer than those of other Loasaceae, based on the vessel element length, which is usually taken as a reliable measurement because vessel elements tend to elongate little or not at all as they mature. Because as noted above *Plakothira* does not seem primitive for Loasaceae in very many features, the long fusiform cambial initials seem not an indicator of primitiveness but rather of paedomorphosis, a feature common in secondarily woody representatives of predominantly herbaceous phylads (for explanation and discussion of paedomorphosis phenomena, see Carlquist 1962). The fact that ray cells are almost exclusively erect also is typical of those secondarily woody groups (Carlquist 1962). A correlative feature in this regard is the tendency for rays to be very wide, tall, and little altered from those of the primary stem (as examination of transections of *Plakothira* wood readily demonstrates). One would expect a much higher degree of ray breakup in genera not characterized by paedomorphosis. The presence of occasional scalariform perforation plates in Loasaceae (Carlquist 1984a; in *Plakothira*, observed only on perforated ray cells) can also be explained as a result of paedomorphosis in accordance with the considerations cited earlier for Valerianaceae (Carlquist 1983). Presence of pits with wide ("gaping") apertures on lateral walls of vessels, as seen in *Plakothira* and some other Loasaceae was cited as an indicator of paedomorphosis earlier (Carlquist 1962), but this may also relate to relatively succulent nature of wood (which in turn does tend to be more common in secondarily woody phylads).

Ecology

Plakothira has notably wide vessels; vessel density is low and vessel element length is great for the family. These three features, combined in the Mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per mm^2) yields the figure 18,124 for *Plakothira frutescens*. This is much greater than for most Loasaceae (Carlquist 1984a). The nearest figures for this ratio are found in *Fuertesia domingensis* Urban (14,398) and *Mentzelia arborescens* (5253).

High mesomorphy ratios are expected for vines on account of the wide vessel diameter characteristic of vines such as *Fuertesia*, in which vessels average 326 μm wide (compared with 92 μm in *Plakothira*). Vessel density in *Fuertesia* is almost double (11) that of *Plakothira* (5.4). Vessel element length is not markedly less in *Fuertesia* (477 μm) than in *Plakothira* (530 μm). For shrubs or trees to exceed vines in mesomorphy ratio figures is rare, and thus the wood of *Plakothira* qualifies as markedly mesomorphic. A subsidiary indication is the very low (1.16) figure for vessels per group in *Plakothira*. A low number of vessels per group in phylads with fiber-tracheids connotes mesic ecology (Carlquist 1984b).

The wood of *Plakothira* exceeds in quantitative values of wood features the values one ordinarily encounters in cloud-forest trees. This circumstance may be related to the elevated mesomorphy ratio values one encounters in Loasaceae as a whole. Certainly one can say that *Plakothira* wood very likely represents an increase in mesomorphy over that of probable ancestors. However, the relatively mesomorphic wood features one finds even in Loasaceae from dry areas may bear a relationship to the succulence of stems in this family (Carlquist 1984a). The thick cortical parenchyma was cited earlier, as was replacement of imperforate tracheary elements by parenchyma as exemplified by *Mentzelia humilis* (Gray) Darlington. The large ray volume of most Loasaceae may be another manifestation of succulence. *Plakothira* certainly has a large ray volume. In addition, the nucleated fiber-tracheids are potentially sites for storage of some water, although that may be discounted because wall rigidity of these cells does not accommodate change in volume so readily as do the thin walls typical of water-storage cells. Only a small amount of starch was observed in the fiber-tracheids of *Plakothira*, but that accumulation may be minimal because of season or plant portion, and photosynthate storage rather than water storage may be the primary function of the nucleated fiber-tracheids.

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